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Aquatic Plant Control Research Program

Assessment of Fish-Plant Interactions

by Eric D. Dibble, K. Jack Killgore, Sherry L. Harrel

Prepared for Headquarters, U.S. Army Corps of Engineers

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U.S. Army Corps of Engineers
Waterways Experiment Station
3909 Halls Ferry Road
Vicksburg, MS 39180-6199

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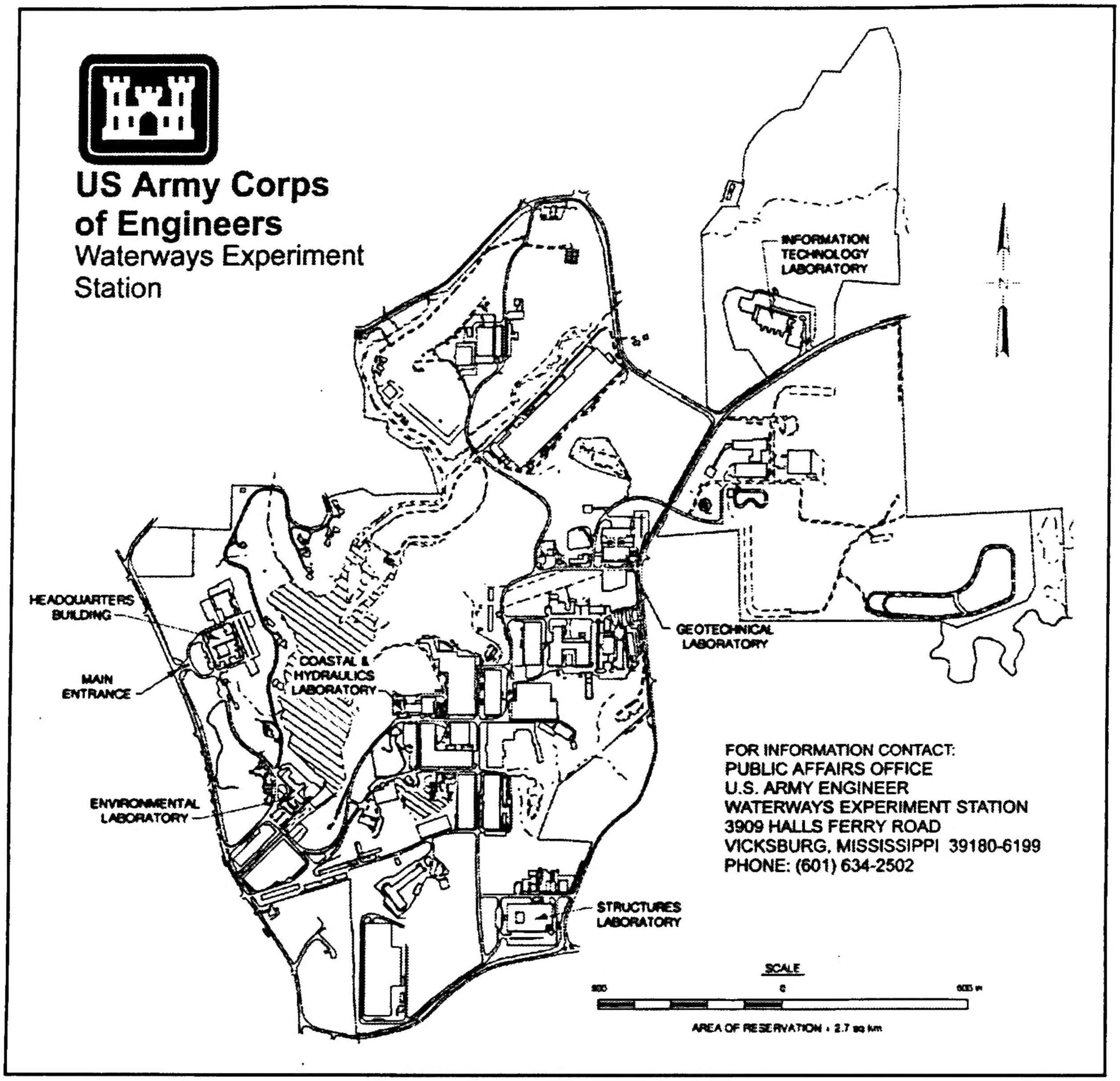

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Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP), Work Unit 32944. The APCRP is sponsored by Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation No. 96X3122, Construction General. The APCRP is managed under the Center for Aquatic Plant Research and Technology (CAPRT), Dr. John W. Barko, Director. Mr. Robert C. Gunkel was Assistant Director for the CAPRT. Program Monitor during this study was Ms. Denise White, HQUSACE.

The Principal Investigator for this study was Dr. K. Jack Killgore, Aquatic Ecology Branch, Ecosystem Research Division (ERD), EL, WES. The report was prepared by Dr. Eric D. Dibble, formerly at WES, now at Mississippi State University (MSU); Dr. Killgore; and Ms. Sherry Harrel, formerly at WES, now at MSU. Technical reviews were made by Dr. Mark Bain, Cornell University; Dr. Jan Hoover, WES; and Dr. Gary Mittelbach, Michigan State University. Results of this study were first published in an article in the American Fisheries Society Symposium 16 titled "Multidimensional Approaches to Reservoir Fisheries Management." Permission was granted by the American Fisheries Society to use this article in the preparation of this report.

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Assessment of Fish–Plant Interactions

Eric D. Dibble[1], K. Jack Killgore, and Sherry L. Harrel[1]

U.S. Army Corps of Engineers, Waterways Experiment Station
Vicksburg, Mississippi 39180-6199, USA

Abstract.—We review the published literature to investigate: (1) the functional importance of aquatic plants to fish, (2) how aquatic plant and fish populations are measured in vegetated habitats, (3) the spatial scale at which previous investigators have quantified fish–plant interactions, and (4) how proximate fish behaviors influence population structure at a macroscale. Based on results of comparative studies, the typical conclusion has been that intermediate levels of plants promote high species richness and are optimal for growth and survival of fishes. Predictable responses by fishes to aquatic plants were noted: vegetated habitats supported higher fish densities than unvegetated areas, aquatic plants led to reduced risk of predation, and structurally oriented fish exploited aquatic plant beds. Pelagic species and benthic omnivores often declined in abundance with increased plant cover, and phytophilic fishes showed rapid population increases during plant growing seasons. When plants occupied an entire water body, fish growth became stunted due to depletion of food resources. These interactions have been assessed largely at a macroscale where aquatic plants are generally mapped from aerial photography or surface measurements and fish data are averaged as standing crop, density, catch per unit effort, or percent abundance relative to plant coverage. Because direct observation of fish in dense plant beds is difficult, few attempts have been made to define and quantify structural complexity of plants at a scale perceived by fishes. We provide aquatic plant attributes potentially important to growth and survival of fishes and suggest that microscale assessment of fish behaviors can be linked to macroscale fishery management strategies through analysis of areal distribution of aquatic plants.

Associations between aquatic plants and fish assemblages are demonstrated in scientific literature with a frequently drawn conclusion that "intermediate" plant densities enhance fish diversity, feeding, growth, and reproduction. Comparison of results among studies can be ambiguous and contradictory, however, because investigators have characterized plant distributions and fish responses on different scales.

We consider two scales in this paper: macro and micro. The method and scale of measurement in relation to fish and plants distinguish these two scales. Fish–plant interactions have been assessed largely at a macroscale using indirect measures. Macroscale refers to either an entire water body or a water body divided into zones (e.g., littoral zone, cove) based on the extent to which shoreline and bottom characteristics influence aquatic habitat (Busch and Sly 1992). Aquatic plants are generally mapped from aerial photography or surface measurements and expressed as hectares of plants, percent coverage, or biomass per hectare. Fish may be collected from specific locations, but data are averaged as standing crop, density, catch per unit effort, or percent abundance relative to areal plant coverage.

Microscale is a measurement of plant complexity at a scale perceived and exploited by an individual or group of fishes. Microscale assessment focuses on behavioral ecology of fishes: the processes by which fishes interact with the environment, and the consequence of behaviors (Noakes and Baylis 1990). In this paper, the location of a microscale sample is referred to as a patch. Rather than areal coverage, underwater architectural features and surface spatial patterns are used to characterize plant complexity within a patch. Behavioral responses by fish include dispersion, preference, and rates of a particular activity (i.e., foraging).

Microscale assessments are uncommon for several reasons. Direct observation of fish in spatially complex habitats is difficult, yet it is the proximate response of individual fish to variation in habitat complexity that determines success in foraging, reproduction, and predator avoidance. Furthermore, most studies have approached fish–plant interactions from human perspectives (e.g., elimination of nuisance growths, enhancement of recreational fisheries) rather than that of individual fish (e.g., exploitation of specific habitats). Previous literature reviews on relationships between aquatic plants and fishes have been limited in scope, emphasized only a few species of plants and fish (Hinkle 1986; Engel 1995), or covered only a specific geographical region (Janecek 1988).

In this paper, we review the literature to investi-

[1]Present address: Mississippi State University, Department of Wildlife and Fisheries, Mississippi State, Mississippi 39762, USA.

gate the functional importance of aquatic plants to fishes, how and at what scale previous investigators have quantified aquatic plants and fishes in vegetated habitats, and how proximate behaviors influence population structure at a macroscale. It is at the macroscale that fisheries management decisions are made. We submit that once proximate behaviors defined at a microscale are quantified, relationships to macroscale fisheries management strategies can be drawn through analysis of areal distribution of aquatic plants. We discuss published studies according to topical areas and identify pertinent conclusions, and include most of the primary literature on fish–plant interactions published over the last 40 years.

Aquatic Plants as Fish Habitat

Areas of Concentration

Many juvenile and adult fishes have been reported in habitats containing aquatic vegetation. Janecek (1988) compiled a list of 112 different species representing 19 families that were collected in aquatic plant beds in the upper Mississippi. The families Clupeidae, Cyprinidae, Ictaluridae, Esocidae, Cyprinodontidae, Atherinidae, Percidae, and particularly Centrarchidae are well-represented (Table 1). When compared to unvegetated areas, vegetated sites contain higher fish densities (Borawa et al. 1979). Up to seven times more fish were collected in areas with plants than in areas without them (Killgore et al. 1989). Similarly, Barnett and Schneider (1974) reported fish density in vegetated habitats as high as 2 million fish/ha. Angling, at least in part, may influence population demography of exploitable fish that are concentrated in vegetated areas (Hoyer and Canfield 1996).

Results of previous studies indicate that fish are attracted to aquatic plants. Sunfish *Lepomis* and bass *Micropterus* abundance were positively related to plant abundance (Forester and Lawrence 1978; Durocher et al. 1984). Submersed vegetation was the key factor in the distribution and habitat use of adult northern pike *Esox lucius* (Cook and Bergersen 1988). Age-0 northern pike were 10-times more abundant in vegetated than unvegetated areas (Holland and Huston 1984). Younger and smaller fishes become more abundant as plant density increases (Barnett and Schneider 1974; Borawa et al. 1979; Moxley and Langford 1985). However, pelagic species, such as white bass *Morone chrysops*, gizzard shad *Dorosoma cepedianun*, and inland silverside *Menidia beryllina*, generally decline in abundance as plants increase in areal coverage (Bailey 1978; Maceina and Shireman 1985; Bettoli et al. 1990).

TABLE 1.—A taxonomic list of fish families and their life stages reported in studies related to aquatic plant habitats. Numbers correspond to individual papers in the list of references.

Fish family	Reference
	Adult
Lepisosteidae	8, 14, 18, 172
Amiidae	15, 18, 78, 148, 172
Anguillidae	18, 100, 166, 172
Clupeidae	4, 17, 15, 18, 95, 100, 115, 148, 172
Salmonidae	11
Cyprinidae	8, 15, 18, 78, 89, 95, 97, 98, 99, 100, 133, 148, 159, 166, 172
Catostomidae	8, 15, 18, 78, 148, 172
Ictaluridae	8, 15, 18, 95, 100, 133, 148, 172, 200
Esocidae	8, 15, 18, 38, 78, 80, 100, 148, 159, 172
Umbridae	143, 184
Aphredoderidae	8, 15
Cyprinodontidae	8, 15, 18, 25, 83, 97, 109, 133, 148, 155, 172
Poeciliidae	8, 15, 100, 133, 172
Atherinidae	15, 16, 18, 21, 89, 90, 100, 133, 166, 172
Cottidae	148
Percichthyidae	15, 18, 100
Centrarchidae	1, 4, 5, 8, 14, 15, 18, 24, 29, 31, 32, 39, 40, 41, 44, 58, 60, 64, 68, 72, 78, 80, 85, 89, 93, 95, 97, 98, 99, 100, 103, 115, 126, 130, 148, 155, 157, 159, 166, 172, 194, 198, 199, 200
Percidae	8, 15, 18, 19, 71, 80, 95, 97, 99, 100, 144, 148, 166, 172, 184, 199
Scianenidae	15, 48
	Juvenile
Salmonidae	75
Cyprinidae	187
Ictaluridae	200
Esocidae	88
Cyprinodontidae	37
Poeciliidae	37
Atherinidae	37
Centrarchidae	1, 2, 14, 32, 37, 58, 60, 64, 68, 71, 72, 78, 93, 103, 106, 129, 130, 131, 133, 200
Percidae	37,187
	Larval
Lepisosteidae	140
Clupeidae	17, 30, 37
Cyprinidae	30, 31, 74, 142, 162
Ictaluridae	30
Catostomidae	162
Esocidae	30, 142
Umbridae	30
Cyprinodontidae	37, 162
Poeciliidae	37, 162
Atherinidae	30, 37, 47
Centrarchidae	30, 37, 47, 74, 140, 162
Percidae	30, 37, 74, 140, 162

Natural senescence of aquatic macrophytes is related to decreased fish abundance in the littoral zone, presumably due to reduction of invertebrate density and cover (Whitfield 1984). Even plant disturbance due to boat traffic decreases fauna and

TABLE 2.—Scale and topical emphasis of fish–plant interaction studies. Numbers correspond to individual papers in the list of references.

Topical emphasis	References
	Macroscale
Fish abundance and composition	1, 8, 14, 17, 18, 37, 54, 58, 74, 85, 89, 100, 123, 125, 133, 140, 141, 142, 146, 148, 172, 184, 195
Habitat use and distribution	1, 37, 38, 74, 77, 88, 96, 125, 129, 140, 146, 151, 172, 187, 194, 198
Foraging and diets	5, 36, 96, 138, 181
Fish growth	14, 32, 39, 77, 115, 117, 129, 138
Reproduction and rearing	1, 30, 37, 47, 74, 128, 133, 140, 175
Plant control effects	4, 5, 14, 15, 16, 17, 31, 32, 33, 34, 35, 59, 60, 64, 110, 115, 117, 154, 167, 171, 180, 181, 189, 190, 199, 200
Recreation and sportfishing	32, 33, 35, 133, 135, 151
Habitat restoration	57
Plant senesence or eutrophication effects	91, 196
Fish induced alterations on plants	176
	Microscale
Foraging and diets	51, 57, 67, 68, 80, 107, 130, 155, 196
Foraging efficiency and predator risk	2, 40, 41, 44, 51, 68, 83, 111, 130, 157, 169, 158, 178, 177, 188, 195
Fish growth	67, 160
Habitat use and distribution	27, 31, 44, 45, 57, 71, 72, 78, 80, 95, 103, 107, 111, 126, 155, 162, 193, 195
Fish effects on plants	24, 122
Fish effects on macroinvertebrates	29, 51, 131, 186, 196
Interspecific competition	80, 103, 131
Plant senescence	196
Behavioral response to pH or DO	166

habitat important to fish communities (Murphy and Eaton 1981).

Foraging Efficiency and Refugia

Aquatic plant beds contain food and provide refuge for younger and smaller fishes. Macroinvertebrate abundance and diversity are higher in aquatic plants than in unvegetated areas because leaves and stems provide substrate for attachment and protection from predators (Gilinsky 1984; Keast 1984; Beckett et al. 1992). Morphology of aquatic plants and depths at which they grow influence production of epiphytes (Cattaneo and Kalff 1980; Keast 1984). Epiphytic invertebrates serve as prey for a variety of fishes (e.g., Centrarchidae, Cyprinodae, Percidae, and Cyprinidontidae) (Hall et al. 1970; Keast 1985a, 1985b; Hoover et al. 1988).

Numerous microscale studies have been conducted on foraging efficiency of fishes (Table 2). Structural complexity provided by plants may reduce predation risk by mediating the extent to which fish interact with prey (Glass 1971; Saiki and Tash 1979; Savino and Stein 1982). Visual and swimming barriers created by dense stems and foliage can reduce foraging success of sunfishes and killifish (Heck and Thoman 1981; Savino and Stein 1982; Dionne and Folt 1991). This effect is due to increased search, encounter, and capture times, as well as reduced encounter, attack, and capture rates, and reduced swimming velocities (Anderson 1984; Diehl 1988). Prey capture rates decline with an increase in structural complexity (Crowder and Cooper 1979b); thus, foraging efficiency declines as habitat becomes more spatially complex.

Some species change foraging tactics as aquatic plants become more complex, or as coverage increases. Largemouth bass foraging in spatially complex habitats may switch from actively pursuing prey to ambushing them, which minimizes the energy cost of prey capture (Savino and Stein 1982). Shade in spatially complex habitats is an important attribute. Shaded areas attract fish (Helfman 1979, 1981; Johnson 1993) and may improve vigilance and foraging behavior by increasing visual acuity (Diehl 1988; Lynch and Johnson 1989).

Fish Growth

The size at which age-0 fish enter their first winter is critical to survival and subsequently influences fish recruitment and production (Gutreuter and Anderson 1985; Adams and DeAngelis 1987). Most studies of aquatic plant effects on fish growth were conducted at a macroscale (Table 2). Their conclusions suggest that aquatic plant abundance mediates fish growth and condition, and that both limited and excessive plant growth may decrease fish growth rates, while moderate levels are optimal.

Excessive plant growth reduces growth and con-

dition of largemouth bass *Micropterus salmoides*, bluegill *Lepomis macrochirus*, black crappie *Pomoxis nigromaculatus*, white crappie *P. annularis*, and redear sunfish *L. microlophus* (Colle and Shireman 1980; Wiley et al. 1984; Maceina and Shireman 1985), presumably by reducing foraging efficiency (Wiley et al. 1984). Colle and Shireman (1980) predicted that largemouth bass growth would significantly decrease in a system with 40% or greater total coverage of aquatic plants relative to a system with less than 40% coverage. Wiley et al. (1984) suggested optimal mean standing crop of pondweeds (e.g., *Potamogeton* and *Najas*) at 52 g dry weight/m^3 would improve foraging efficiency in largemouth bass. Total removal of aquatic plants increases growth of largemouth bass, black and white crappies (Maceina et al. 1991), bluegill, and redear sunfish (Bailey 1978), and may alter foraging behaviors of largemouth bass by initiating piscivory sooner in smaller age-classes, resulting in rapid growth (Bettoli et al. 1992).

Young sunfishes and perch *Perca fluviatilis* often showed the opposite trend from larger piscivores; increased vegetation density was positively related to their growth (Gerking 1962; Hall and Werner 1977; Blindow et al. 1993). When plants were sparse, competition increased, resulting in slower growth rates due to reduced caloric intake (Mittelbach 1981; Mittelbach and Chesson 1987; Diehl 1993). However, stunted growth also occurred when plants occupied the entire water body, particularly in shallow systems without any deep, unvegetated areas (Colle and Shireman 1980; Engel 1988).

TABLE 3.—Methods and parameters used to classify aquatic plant habitats. Numbers correspond to individual papers in the list of references.

Method or parameter	Reference
Aerial photography, digital imagery	13, 54, 55, 59, 82, 92, 108, 113, 116, 121, 170, 199
Circular core	81, 116, 120
Divers	4, 24, 42, 53, 59, 85, 95, 108, 111, 118, 120, 132, 146, 169, 196, 201, 202
Fathometer, acoustics	53, 108, 116, 118, 173, 179, 182
Grab, grapnel, dredge, rake	61, 136, 156, 165, 174
Plant removal (by hand)	20, 32, 66, 202
Quadrat	42, 52, 54, 59, 88, 100, 108, 118, 120, 132, 145, 146, 149, 161, 167, 196, 199
Transect	22, 23, 24, 32, 75, 85, 104, 111, 118, 120, 136, 173, 196
Aerial coverage, % composition	4, 14, 23, 32, 38, 61, 75, 85, 104, 135, 148, 195, 199
Biomass measurements	20, 23, 42, 52, 89, 92, 100, 104, 108, 111, 118, 139, 146, 147, 149, 156, 161, 163, 165, 167, 179, 199, 202
Biovolume	182
Canopy, plant density	42, 74, 100, 104, 165
Submerged versus emerged	121, 126
Mat buoyancy	145
Plant morphology	20, 111, 145, 147
Plant weight, wet	81, 145
Presence and absence	4, 14, 32, 31, 98, 106, 140, 162, 172, 183, 198

Spawning and Rearing

Many North American fishes are obligatory plant spawners; these include members of Amiidae (e.g., *Amia*), Esocidae (e.g., *Esox*), Cyprinidae (e.g., *Cyprinus*, *Cyprinella*, *Notemigonus*), Catostomidae (e.g., *Ictiobus*), Cyprinodontidae (e.g., *Fundulus*), Atherinidae (e.g., *Labidesthes*), Umbridae (e.g., *Umbra*), Centrarchidae (e.g., *Elassoma*), and Percidae (e.g., *Perca*, some *Etheostoma*) (Pflieger 1975; Robison and Buchanan 1988). However, most empirical data on spawning success relative to structural complexity and plants come from studies of adult sport fishes that construct nests (i.e., largemouth bass and bluegill).

Adult largemouth bass and bluegill select sites protected from wave action (Tester 1930; Kramer and Smith 1962; Miller and Kramer 1971) and keep their nests cleared of vegetation, sometimes influencing littoral vegetation spatial patterns (Carpenter and McCreary 1985). Although nest spawners successfully spawn in areas devoid of vegetation, they prefer sites with aquatic plants or some other type of structure nearby for refugia (Vogele and Rainwater 1975; Mesing and Wicker 1986; Hoff 1991; Annett et al. 1996, this volume). However, dense vegetation throughout the littoral zone can hinder spawning adults by decreasing the availability of nest sites (Colle and Shireman 1980).

Aquatic vegetation is used as nursery habitat for larvae by at least 12 families (Table 1). Larval stages of sunfish, brook silverside *Labidesthes sicculus*, yellow perch *Perca flavescens*, golden shiner *Notemigonus crysoleucas*, northern pike, and certain species of darters are more abundant in vegetation than in open water (Floyd et al. 1984; Gregory and Powles 1985; Paller 1987; Dewey and Jennings 1992). Some species exhibit ontogenetic shifts in habitat use. For example, prolarvae of yellow perch prefer shallow, dense macrophyte areas, while postlarvae prefer deep, low-density macrophyte zones (Gregory and Powles 1985).

Quantifying Fish–Plant Interactions

Quantifying Plants

Measurements of plant biomass, area coverage, percent species composition, and presence or absence are typically used to quantify growth characteristics of aquatic plants (Table 3). Aerial photography, and more recently digital imaging using geographic information systems (GIS) (Lukens 1967; Harvey et al. 1988; Jennings et al. 1992; Marshall and Lee 1994), are remote sensing techniques to map and estimate acres of aquatic plants at the macrohabitat scale. Ground measurements (e.g., quantifying morphology of individual plants or small groups of plants and use of quadrant and transect data) are common (Table 3), and these data are often extrapolated to the entire system (Forsberg 1959; Edwards and Moore 1975; Cassani and Caton 1985; Smart and Barko 1988). Plant biomass has been quantified using direct hand removal of plants, modified dredges, grabs, and rakes within defined areas (Sabol 1984; Sliger et al. 1990) (Table 3). Where water conditions are favorable, samples are taken directly by divers using scuba or snorkel gear (Kautsky et al. 1981; Pringle 1984; Downing and Anderson 1985; Machena and Kautsky 1988).

Architectural features are microscale assessment of morphology and plant spacing. A fathometer has been used to estimate plant height and map aquatic plant distributions (Maceina and Shireman 1980; Maceina et al. 1984; Schloesser and Manny 1984; Stent and Hanley 1985; Duarte 1987; Pine et al. 1989; Thomas et al. 1990). A more recent approach to quantification of plant architecture is to measure interstitial spaces and leaf and stem morphology (Johnson et al. 1988; Lynch and Johnson 1989; Walters et al. 1991; Lillie and Budd 1992; Wychera et al. 1993; Dibble and Killgore 1994).

Quantifying Fish in Aquatic Plants

Divers have successfully quantified relative abundance of fish species in the littoral zone (Table 4). Under suitable conditions (i.e., high water clarity and moderate plant density), divers can rapidly census fish populations and measure species composition and abundance in habitats that are difficult to sample with traditional methods (Northcote and Wilkie 1963; Keast and Harker 1977; Heggenes et al. 1990; Dibble 1991). However, excessive plant growth may hinder direct observation of fish (Heggenes et al. 1990; Rodgers et al. 1992).

Boat-mounted electroshockers are commonly used to sample fish in aquatic plants (Table 4), but dipping efficiency is reduced in dense plant beds (Killgore et al. 1989). Frame electroshocking equipment used to sample fish in rivers (Bain et al. 1985a) has been modified for use in dense vegetation (Dewey 1991; Vadas and Orth 1993). A time delay between disturbance (i.e., setting up the frame electroshocker) and the sample can decrease the effect of fright response by fish (Bain et al. 1985a).

A variety of nets has been used to sample fish in aquatic plants (Table 4). Pop nets and drop nets measure distribution, diversity, and abundance of adult and juvenile fishes in densely vegetated areas where traditional methods (i.e., seining and electrofishing gear) are ineffective (Freeman et al. 1984; Morgan et al. 1988; Serafy et al. 1988; Dewey et al. 1989; Espegren and Bergersen 1990). Underwater observations of pop nets in use in pools and reservoirs demonstrated they were accurate for sampling small fish in complex habitats (Larson et al. 1986), and pop nets may be one of the better gears to collect young fishes in aquatic plants.

Vegetated areas have been blocked off with nets

TABLE 4.—Methods and tools used to quantify fish in or near vegetated areas. Numbers correspond to individual papers in the list of references.

Method	Reference
Angling	203
Belt transect	24, 78, 98, 138, 195
Divers	24, 48, 56, 78, 98, 99, 137, 138, 152, 195, 203
Drop or throw nets	7, 8, 28, 30, 65, 192
Echosounder	11
Electro-shocker and block net	10, 119, 185
Electro-shocker	5, 6, 14, 31, 32, 39, 75, 105, 152, 183, 198
Explosives	3, 9, 10, 63, 105, 127
Fyke nets	184
Gill nets	14, 38, 85, 127, 146, 187, 196
Helicopter	137
Hose pump or net	140
Light trap or minnow trap	47, 74, 85, 95, 107, 184
Modified nets	14, 196
Modified traps	65, 85, 199
Popnets	62, 46, 100, 132, 166, 167, 168
Push net	30, 124, 162
Radio telemetry	5, 31, 38, 126, 183, 198
Rotenone and block net	18, 54, 125, 129, 172
Rotenone	1, 4, 48, 105, 115, 127, 133, 137
Seine	14, 46, 65, 88, 89, 97, 99, 132, 152, 185
Shore observations	137
Stationary nets	14
Strip counts	98, 99
Tow nets	37
Trapnetting	85
Trawl	148
Underwater camera	11, 49, 56

and sampled with rotenone (Lambout 1959), but collection efficiency decreased as plant density increased (Shireman et al. 1981). Catch depletion techniques, in which a series of samples are collected and differences among samples are plotted on a depletion curve to estimate abundance, eliminated the need to remove fish from the net (Morgan et al. 1988; Maceina et al. 1995). Sampling with rotenone in vegetated areas enclosed with a block net was less expensive and provided a more realistic assessment of largemouth bass than cove rotenone sampling (Maceina et al. 1995).

Seines were commonly used to sample fishes near vegetation (Table 4), but were difficult to use in dense plant beds. Light traps were efficient for determining larval fish abundance and species composition in aquatic plants (Faber 1981; Gregory and Powles 1985). Modified ichthyoplankton nets have been used to sample larval fishes in structurally complex habitats where traditional tow nets could not be easily used (Barnett 1973; Meador and Bulak 1987).

Discussion

Based on our assessment of the literature, there are predictable responses by fish in relation to aquatic plants, albeit mostly derived from macroscale studies of plant control operations (Table 2). Vegetated areas support fish densities from 15,000 to over 2 million fish/ha, higher than unvegetated areas. Structurally oriented fish exploit aquatic plant beds, with juvenile sunfishes being numerically dominant in vegetation in most North American water bodies. In contrast, pelagic species and benthic omnivores (e.g., Catostomidae) often decline in abundance as plants increase in areal coverage. At least 19 families of freshwater fishes have been documented to occupy vegetated habitats during at least one of their life stages.

Aquatic plants, like other sources of structural complexity in habitats, reduce risk of predation by providing refugia for smaller fish and mediating the extent to which fish interact with prey. Both sight and bottom feeders are hampered by interference from plants and stems. Phytophilic fishes increase rapidly during the plant growing season, but if plants occupy an entire water body, growth becomes stunted because food resources are depleted.

Most comparative studies of plant and fish abundance conclude that intermediate vegetation levels, defined as 10–40% coverage of study sites, including areas ranging from individual coves to entire water bodies, promote high species richness and are optimal for growth and survival. Theoretically, because plants provide spatial complexity, intermediate densities may promote community stability by providing habitat heterogeneity (Stenseth 1980), yet mechanisms governing population dynamics as a function of plant coverage remain speculative. In addition, the lack of consistent measures of plant coverage and the problem of defining intermediate density at different scales hamper comparisons among aquatic systems and lead to variable responses by fish populations.

Fish responses are more predictable at the extremes of plant coverage. When aquatic plants cover an entire water body, foraging by piscivores is hampered by stems and leaves, small phytophilic insectivores increase in abundance due to lower predation and higher prey abundance, and spawning by nest builders is confined to limited areas that may increase competition and decrease spawning success. Conversely, water bodies that lack vegetation generally have lower densities of littoral fishes, although standing crop may not differ substantially, and fishes become more aggregated (Aboul and Downing 1994). Comparisons of vegetated and unvegetated areas within the same water body generally show that fish assemblages in unvegetated areas have lower densities and fewer species.

Long-term studies that monitor changes in fish populations as a function of changing plant coverage provide important insight into fish–plant interactions. When plants were completely eliminated in Lake Conroe, Texas, the littoral fish community shifted from sunfish and shad to include sizeable numbers of cyprinids, inland silversides, and channel catfish *Ictalurus punctatus* (Bettoli et al. 1993). Scott (1993) reported shifts in fish assemblages over a 30-year period as Eurasian watermilfoil *Myriophyllum spicatum* increased in Chickamauga Reservoir coves, Tennessee. Midwater insectivores (e.g., golden shiner, sunfishes, brook silverside, yellow perch) and ambush predators (e.g., largemouth bass) increased in abundance while benthic insectivores omnivores (e.g., smallmouth buffalo *Ictiobus bubalus*, spotted sucker *Minytrema melanops*, channel catfish, and freshwater drum *Aplodinotus grunniens*) declined in abundance. Others found that plant reduction had little effect on fish populations, and that factors other than aquatic plants may have greater effect (Bailey 1978). Studies of the effects of plants on specific fish species also were inconclusive when considered together. Wiley et al. (1984) and Noble (1981) showed increases in the number, recruitment, and survival of catfish after plants were

removed, whereas, Borawa et al. (1979) reported opposite trends.

Studies of shifts in fish assemblages following changes in plant coverage have produced conflicting results. Most studies are based on indirect measurements of causal mechanisms regulating fish populations (e.g., Kushlan 1974; Freeman et al. 1984; Gregory and Powles 1985), which may lack the precision required to determine important fish–habitat relationships in vegetated areas. Consequently, proximate habitat factors and fish behavioral responses are seldom quantified.

The choice of scales for observing natural interactions must be a primary consideration in study design. Large-scale measurements generally have low resolution but are inherently stable whereas small-scale, site-specific measurements have high resolution and low stability (Busch and Sly 1992). We suggest that vegetated water bodies be viewed and described by first studying their individual parts. Through integration of the parts, biological processes can be defined. This approach is analogous to patch analysis. However, few attempts have been made to define and quantify habitat variables at a scale important to fishes. Microscale measurements have been used to quantify fish habitat in streams (Orth and Maughan 1982; Price 1982; Bain et al. 1985b), and similar approaches are needed to delineate habitat criteria for aquatic plants in reservoirs.

A variety of structural and functional habitat criteria measured at a microscale can be used to better evaluate aquatic plants as fish habitat (Table 5). For example, aquatic plant species differ in morphology and spatial distribution (Lillie and Budd 1992; Wychera et al. 1993; Dibble et al. 1996), and these differences likely influence fish behavior. Young bluegill preferred smaller interstitial spaces (40–150 mm) within structural habitat over larger ones (350 mm), and largemouth bass preferred structure with medium-sized spaces (150 mm) (Johnson et al. 1988). Thus, proximate or microscale studies that quantify fish behavioral responses such as habitat preference, foraging efficiency, predator avoidance, and social attraction in vegetated areas are required to clarify the role of aquatic plants as fish habitats.

Aquatic plant management is usually performed on a macroscale which necessitates the management of fisheries on a compatible scale. For example, there may be a trade off of catching fewer but larger fish at lower plant coverage (Maceina and Reeves 1996). Plants are mapped from remotely sensed data and GIS provide estimates on the areal coverage of submersed, floating, or emergent growth forms. Because boundaries of plant beds can be delineated from remotely sensed data (Marshall and Lee 1994), heterogeneity of different patches of plants can be identified. Thus, remote sensing techniques can be used to spatially extrapolate fish–plant relationships developed at the microscale to a larger scale.

TABLE 5.—Microscale studies on structural and functional role of fish habitat and variables potentially important to evaluate the role of aquatic plants. Numbers correspond to individual papers in the references section.

Variable addressed	Reference
	Structural
Interstitial size and abundance	93, 111, 114, 178
Plant morphology and architecture	20, 26, 51, 111, 153, 197, 202
Plant diversity	194, 197
Plant strata	58, 59, 111, 197
Shade effects	50, 84, 94, 111, 114, 197, 202
Spatial complexity	2, 20, 39, 40, 41, 50, 68, 69, 93, 94, 158, 164, 194
Stem density	2, 20, 40, 41, 51, 69, 71, 72, 83, 158, 160
	Functional
Effects on competition	103, 131
Effects on reproduction and recruitment	69, 76, 86, 101
Influence on foraging	2, 29, 39, 40, 41, 44, 50, 51, 59, 68, 69, 71, 76, 77, 83, 87, 130, 13 1, 155, 157, 158, 165, 177
Prey resources and availability	12, 26, 50, 51, 58, 59, 68, 70, 73, 77, 79, 95, 102, 103, 112, 165, 131, 141, 142, 150, 153, 164, 177, 178, 191
Refugia	39, 40, 41, 43, 45, 68, 72, 77, 83, 87, 131, 134, 155, 157, 158, 164, 188

In conclusion, most investigations of fisheries resources associated with aquatic plants emphasize static responses of only a few fish species at gross spatial levels. Conversely, most behavioral data on fish–plant interactions come from studies of small sunfishes. Few empirical data are available to bridge the theoretical predictions of responses by fish in plants at a microscale to population responses of fishes at a macroscale. Addressing scale, structural variables within aquatic plants, and fish behavior will allow direct effects of aquatic plants to be identified and make it possible to extrapolate results. The role of aquatic plants as fish habitat and their value as a management tool in reservoirs then can be better defined.

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13. ABSTRACT *(Maximum 200 words)*

The published literature was reviewed to investigate (a) the functional importance of aquatic plants to fish, (b) how aquatic plant and fish populations are measured in vegetated habitats, (c) the spatial scale at which previous investigators have quantified fish-plant interactions, and (d) how proximate fish behaviors influence population structure at a macrolevel. Based on results of comparative studies, the typical conclusion has been that intermediate levels of plants promote high species richness and are optimal for growth and survival of fishes. Predictable responses by fishes to aquatic plants were noted: vegetated habitats supported higher fish densities than unvegetated areas; aquatic plants led to reduced risk of predation; and structurally oriented fish exploited aquatic plant beds. Pelagic species and benthic omnivores often declined in abundance with increased plant cover, and phytophilic fishes showed rapid population increases during plant growing seasons. When plants occupied an entire water body, fish growth became stunted due to depletion of food resources. These interactions have been assessed largely at a macroscale where aquatic plants are generally mapped from aerial photography or surface measurements and fish data are averaged as standing crop, density, catch-effort, or percent abundance relative to plant coverage. Because direct observation of fish in dense plant beds is difficult, few attempts have been made to define and

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quantify structural complexity of plants at a scale perceived by fishes. Aquatic plant attributes potentially important to growth and survival of fishes are provided, and these authors suggest that microscale assessment of fish behaviors can be linked to macroscale fishery management strategies through analysis of aerial distribution of aquatic plants.